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ODOR DIFFERENTIATION IN *LAGENANDRA OVATA* (ARACEAE)

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Abstract *Cryptocoryninae* have highly synorganised inflorescence, which exhibit differential odor production. In Lagenandra, the long - distance attracting stench is produced by the upper part of the spathe. The anthers and the sterile clubs above the female flowers produce a fruity odor filling the lower part of the inflorescence (kettle). The sterile organs on the spadix have special features, such as dense, starch containing tissue with high metabolic activity, positive neutral red reaction, papillae, and rich supply with vascular bundles. Similar inflorescence architecture and differential odor production are known from other Araceae.

Key words *Lagenandra ovata*, *Cryptocoryninae*, odor, odor differentiation.

INTRODUCTION

1. Systematics

According to Engler (1920a, 1920b) and Bogner et Nicolson (1991), *Lagenandra* is included with *Cryptocoryne* in the subtribe *Cryptocoryninae* (Araceae, *Aroideae*). The position of *Cryptocoryninae* may change in the near future (French, personal communication; Boyce, personal communication).

2. Inflorescence Architecture at Anthesis

Cryptocoryninae show highly synorganised inflorescence (Figs 1 - 3, 5, 6). Vogel (1963) designates *Cryptocoryne* as possessing the most highly evolved pitcher traps. He identifies Cryptocoryne as myophilous by the odor and by the colors of the spathe (olive, brown). General descriptions of the inflorescence architecture and the floral morphology of *Cryptocoryninae* are by Engler (1884, 1920b). In this study, the terminology for the different parts of the inflorescence of Lagenandra is based on De Wit (1970, 1982) with some modifications (Figs 3,6). These authors sometimes differ in the interpretation of the individual organs, especially the sterile and the male ones.

At anthesis, the spadix of *Cryptocoryninae* is completely hidden by the spathe. Typically the spathe is divided by a constriction into an upper, open chamber and a lower chamber (kettle, Figs 2, 3). The kettle is congenitally fused into a tube around the spadix (Figs 1, 23), as in many other members of the *Aroideae* (Engler, 1884, 1920b; De Wit, 1970). In most species of *Cryptocoryne*, the margins of the spathe are postgenitally fused into a tube (Fig. 31), but in *Lagenandra*, the margins open completely and the inflorescence resembles that of C. spiralis (Figs 4, 23). The unfused part of the spathe is elongated into a spiral. It is upright and in *L. ovata* and *L. praetermissa* (Figs 1 - 3, 23) it ends in a massive tip, similar to a tail (Engler, 1920a, 1920b; De Wit, 1982).

The spathe above the constriction expands in *L. ovata* and, to a lesser extent, in *L. praetermissa*, to form an extensive chamber (Figs 2, 3, 23). In *L. ovata*, the constriction of the spathe is extended to a septum, like a roof (Figs 3, 5). In *L. praetermissa*, this roof is not as elaborated. Still, the spathe forms a fold surrounding the passage to the kettle (Fig. 23). In all *Cryptocoryninae*, the upper chamber and the lower kettle are connected by a very narrow bottleneck passage - way (Figs 5, 6, 28).

1). Appendix

The appendix terminal to the inflorescence axis is typical for Aroideae (Engler, 1884, 1920a, 1920b; Vogel, 1963; De Wit, 1982). In *Cryptocoryninae* the spathe encloses the appendix by a valvule (De Wit, 1982), which is a flap – like outgrowth of the spathe into the spathe chamber (Figs 5, 6, 27, 28, 32). By this enclosure, the spathe is fused to the appendix. This fusion is illustrated by Engler (1920b) and described by De Wit (1970, 1982) for *Cryptocoryne*. However for *Lagenandra* it has not been described in detail and its functioning mechanism is not understood.

2). Fertile Flowers

The female flowers (Figs 5, 14, 16) are reduced to simple gynoecia with a stout style and a broad, sessile, papillate stigma (Engler 1920b). On their lateral sides, the flowers bear irregular mounds, the function of which is not known (De Wit, 1982). The male flowers consist of one or two sessile anthers with two thecae each (Figs 9 – 12), and a tubular stomium for each theca (Engler, 1920a; De Wit, 1982).

3) Clubs

Between male and female flowers, there are sterile structures (Engler, 1884, 1920a, 1920b; De Wit, 1970, 1982). They are club – shaped (Figs 6, 16, 18, 19). Their homology in *Lagenandra* is not clearly understood (Fig. 17).

3. Pitcher Trap Flowers and Odor in General

The most comprehensive study of osmophoric tissues in several families was done by Vogel (1963). In addition to Araceae, carrion – like smell and pollination by dipters and coleopters, combined with pitcher trap blossoms is well known in *Aristolochiaceae* (Cammerloher, 1923; Vogel, 1963; Endress, 1994), *Asclepiadaceae* (*Ceropegia*, Vogel, 1963), *Hydnoraceae* (*Hydnora africana*, Burger et Munro, 1988) and *Rafflesiaceae* (Beaman *et al*, 1988; Banziger, 1991).

In *Ceropegia*, special osmophores are formed to attract pollinators (Vogel, 1963). In *Aristolochia*, the corolla margin is either differentiated into a continuous osmophore (*A. cordiflora*) or an extension is formed (*A. trilobata*, Vogel, 1963). In *Hydnora africana*, special ‘bait bodies’ are responsible for the smell production (Burger et Munro, 1988).

Osmophores often show a club – like form (‘Palp osmophores’, Vogel, 1963). The yellow color is a character of osmophores, in general. It is known from osmophores in *Aristolochia cordiflora*, Orchids, *Ceropegia* (Vogel, 1963) and it is present in the appendix of Araceae, e.g. of *Arum* by chromatophores (not carotinoids, Vogel, 1963), of *Amorphophallus*, *Alocasia*, *Spathiphyllum*, (Vogel, 1963, and personal observation), and of *Sauromatum*, (Chen et Meeuse, 1971).

Anatomical and cytological features of osmophores were described by Knoll (1926), Van Herk (1937), Vogel (1963), Chen et Meeuse (1971), and Bay (1996). The tissue is served by many vascular bundles (Vogel, 1963, for *Ceropegia* and *Arum*). These bundles are responsible for the replacement of water, which is lost by the strong transpiration during odor release. However, they are composed of phloem to a large extent. Thus they import energy substrate (Vogel, 1963).

The osmophoric tissue is differentiated into an energy storing, scent – synthesizing mesophyll and a papillate epidermis (‘secretory epithelium’, ‘papillate epithelium’ for the appendix of *Arum*, Vogel, 1963). According to these authors, the cells in the mesophyll show dense cytoplasm, an expanded nucleus, and a visible nucleolus. The mesophyll cells contain starch or fatty oils (Vogel, 1963; Chen et Meeuse, 1971; Bay, 1996). Vogel (1963) describes a high protein content, due to high enzymatic activity. The epidermis contacts the air with a thin cuticula. The epidermis does not store starch (Vogel, 1963). In the epidermis of *A. maculatum* and *Helicodiceros muscivorus* the nucleus is also polyploid and enlarged, but shows no nucleolus in contrast to the mesophyll tissues (Vogel, 1963).

These special features of osmophores are associated with the elevated metabolic activity and transcription rate (Vogel, 1963; Matile, 1958; Chen et Meeuse, 1971; Bay 1996) and are typical for secretory tissues in general (Vogel, 1963). Odor production is often accompanied with heat production (Knoll, 1926; Matile, 1958; Vogel, 1963; Smith et Meeuse, 1966; Chen et Meeuse, 1971; Meeuse *et al*, 1984; Bay, 1996).

Typically, odor and heat production only last for some hours or one day. After anthesis, the cytoplasm collapses and the energy reserve has been consumed. Neutral red reacts negatively, indicating osmophores are no longer active (Vogel, 1963).

4. Odor Composition

Pitcher trap blossoms are mostly pollinated by dipters and coleopters, which react instinctively to osmophoric signals and show little learning behavior (Vogel, 1963; Rice, 1977; Pellmyr et Patt, 1986; Beaman *et al*, 1988; Banziger, 1991; Patt *et al*, 1992).

These blossoms emit a smell imitating a potential food source or oviposition sites, in respect to the reproduction ecology of the insects found in the traps (Vogel, 1963; Beaman *et al*, 1988; Banziger, 1991; Kite, 1995; Bay 1996). Therefore, odors such as of ripe fruits, dung, carrion, and fungi are often found. The compounds found mostly are steroids, (Vogel, 1963; Pellmyr et Patt, 1986) terpenoids, ethereal oils amides, amines, and indoles (Vogel, 1963; Bay, 1996), skatole, cadaverine, putrescine (in *Sauromatum guttatum*, Chen et Meeuse, 1971; Smith et Meeuse, 1966).

Vogel (1963) notes that odor composition varies strongly between even closely related taxa. Especially species of *Arum* show a large variety of different odors (fruit – like, cheese – like, urine – like, fecal), obviously a specialization to specific pollinators (Vogel, 1963, personal observation). Headspace analysis carried out on *Arum maculatum* by Kite (1995) uncovered 56 components.

Patt *et al*. (1992) concluded that "aroids use complex floral morphology in tandem with floral odors to attract and manipulate (...) pollinators" and that a highly specialized mutualism, as in *P. virginica*, is expected for other aroids, too. The high diversity of odor compounds leads to the conclusion, that Araceae are very flexible in their biochemical pathway in order to respond to specific pollinator selection.

Odor compounds of *Cryptocoryninae* are unknown. Vogel (1963) mentions different odors in *Cryptocoryne*: *C. griffithii* and *C. undulata* smell repulsive while *C. ciliata* smells fruity (terpenoids, etheric oils). De Wit (1970) writes, that the carrion – like smell of *Cryptocoryne* sometimes turns to sweet. Pollinators of *Lagenandra* are unknown. For *Cryptocoryne*, De Wit (1982) mentions *Diploneura* (*Phoridae – Diptera*). In *Cryptocoryne cf. consobrina* from Kerala (India), *Sphaeroceridae* ('dungflies') were found (personal observation).

The appendix is the typical osmophore in *Araceae*. In Aroideae with differential odor production it normally produces the fecal odor. But there are alternatives: *Anthurium* has been described as used by male euglossine bees as perfume source (Dodson, 1966; Dressler, 1968; Zucchi *et al*, 1969; Croat 1980). Perhaps the waxy, massive petals are osmophores. In *Spathiphyllum*, the conical style is the main osmophore (Vogel, 1963; Lewis *et al*, 1988; Williams et Dressler, 1976). The spathe is able to acquire the osmophoric function, too: in *Helicodiceros*, the spathe has a fruity odor, different from that of the appendix (Vogel, 1963). In *Lysichitum* (Chen et Meeuse, 1971), in *Symplocarpus* and in *Lasia* (Vogel, 1963), the entire spathe produces odor. At least some part of the spathe produces odor in *Colocasia*, *Remusatia* (personal observation), *Typhonium* (violet – like), and *Arum* (Knoll, 1926). In some members of *Arisaema*, in *Arisarum proboscideum* (Vogel, 1963) and probably in *Ambrosina bassii* (personal observation), the spathe tips are specialized osmophores.

In *Cryptocoryne griffithii* and *C. ciliata*, the collar ('flag', De Wit, 1982) terminating the spathe tube is an osmophore with a conspicuous secretory epithelium (Vogel, 1963). The same is probably true for other species of *Cryptocoryne* (personal observation). Further, *Cryptocoryne ciliata* has a yellow osmophore on the inner surface of the spathe (Vogel, 1963). Vogel (1963) describes the anatomy of these spathe osmophores and their function as identical to the axial appendices of other aroids, while the appendix of *Cryptocoryne* is neither an osmophore, nor is it thermogenetic.

5. Differential Odor Production

In some sapromyophilous pitcher trap blossoms more than one kind of osmophores is found. Vogel (1963) describes two different types of osmophores in *Aristolochia* aff. *cordiflora*: the perianth margin and a yellow disk at the floral entrance. The perianth margin does not contain significant amounts of starch (Vogel, 1963), while the yellow disk is solid, contains starch, and produces heat and odor. Vogel (1963) gives no explanation why a plant builds two kinds of osmophores at two different places of the blossom. For *Aristolochia* aff. *cordiflora*, Vogel (1963) describes two types of odor, one fecal and one fruity. According to him, these different odors are produced by different individuals. Still, it would be interesting to know, whether the two observed odors are generated by the two different organs.

In *Rafflesia kerrii* Banziger (1991) found a differential odor production. Outside the blossom, fecal odor functions as a long distance attractant produced by the perianth, while inside the flower, a fruity odor is perceptible, probably produced by the central disk. Both spaces are separated by a diaphragm.

In *Sauromatum guttatum*, Meeuse *et al*. (1984) discovered the "mild climacteric and fragrance production in the yellow club shaped organs". The sterile clubs are arranged above the female flowers and contain starch and amylose – phosphatase. Starch disappears during anthesis and (– pinene and limonene are found to be secreted by the clubs. These substances contrast as sweet – fruity smelling odors to the fecal indole – skatole odor of the appendix caused by indole and other compounds.

Kite (1995) showed differential odor production within the inflorescence of *Arum maculatum*. He found different substances in the spathe chamber and in the upper air of the appendix: while germacrene and viridiflorine, sesquiterpenoids and benzenoids are restricted to the spathe chamber, p – cresol, indole, monoterpendoids and 2 – heptanone are characters of the appendix head space.

6. Questions for *Lagenandra*

Is there an osmophoric differentiation in the inflorescence of *Lagenandra*? What are the specific osmophores and what are the ecological deductions?

MATERIAL AND METHODS

Inflorescence of *L. ovata*, *L. praetermissa*, *Cryptocoryne usteriana*, *C. spiralis*, *and C. retrospiralis* were studied. They are all cultivated in the greenhouses of the Institute for Systematic Botany and Botanical Garden of the University of Zurich. Specimens of the same clone of *C. spiralis* and *C. retrospiralis* cultivated by J. Bogner in Munich were also used. *C. cf. consobrina* was collected by Prof. Dr. C. D. K. Cook in Kerala (India). Voucher specimens were deposited at the herbarium of the institute (Z – ZT).

Methods included classical microtome sectioning, with embedding in parablast and GMA (lgersheim et Cichocki, 1996), and SEM studies. Osmophors were detected by vital staining and bright field observation, since it was found to be a reliable indicator for osmophors (Vogel, 1963), in combination with microscopic observations and by investigating the odor.

To determine the parts of the inflorescence and their odor, freshly anthetic inflorescence were tested with the nose. The inflorescence were opened longitudinally by an oblique cut with a razor blade, and the exposed spathe sections (upper chamber, passage way and kettle with spadix) examined with the nose. Following the description by Vogel (1963), the inflorescence were then divided into different parts: upper spathe chamber (without passage way), the passage way region (plus valvule), the spathe part of the kettle wall, the fertile, male part of the spadix, the top of the female part of the spadix containing the sterile clubs (and some stigmata), and the major part of the female spadix (without sterile organs).

These elements were enclosed into separate glass containers (snap caps), which has been cleaned with tap water and dried, until no odor contamination was perceptible. The first incubation in the snap caps lasted one hour at 20℃. Then the lid was opened and the enclosed air was examined. The lid was closed again and the incubation repeated until no further change occurred.

RESULTS

1. Spathe

In *Lagenandra ovata* and *L. praetermissa*, dense verrucate emergences are visible on the outside surface of the spathe (Figs 1 – 3). They are arranged in longitudinal rows. In *L. ovata*, the inner surface of the spathe is covered by anastomosing, horizontal ribs (Figs 22, 28). Inside, the spathe surface of *L. praetermissa* is covered with such ribs, too. But they are tiny and lighter than in *L. ovata*, so the spathe surface looks almost smooth. Along the margins of the spathe, and especially densely on the septal roof, these ribs are extended into verrucate emergences, in *L. ovata* (Figs 2, 3, 5, 22, 24, 28). They are similar to those on the external surface, but considerably longer and apical only light colored (Fig. 24).

The margins of the spathe overlap in a spiral and loosen completely at anthesis. The inner margin continues basely inside the spathe suture by an extension (Figs 27, 28, 32). It bends spirally, surrounding the upper part of the spadix and tightly attaching to the appendix (Figs 6, 27 – 29, 32). Thereby, it forms a flap (valvule, De Wit 1970), stabilizing the spadix and limiting the narrow passage way towards the spadix (Figs 5, 6, 27, 28).

In microscopic dimensions, the epidermis of the spathe valvule and the passage way bear acute papillae oriented downward (Engler, 1920b) (Figs 25, 26). Acute papillae as on the epidermis of the spathe are also found along the tube of *Cryptocoryne usteriana* and in the basal region of the postgenitally fused part of the spathe in *Lagenandra ovata* (Fig. 26). In *L. ovata* they do not occur symmetrically on both margins: the outer margin (in respect to overlapping in the bud) bears reduced verrucate emergences, the inner on one is covered by papillae (Fig. 26).

2. Appendix

The appendix is enclosed within the spiral of the valvule (Figs 5, 6, 29). In the center of this spiral, an opening remains, where the appendix tip contacts the upper spathe chamber only with a very little part of its tip (Figs 28, 30, 32). In *Lagenandra ovata*, *L. praetermissa* and *Cryptocoryne* cf. *consobrina*, there is no permanent postgenital fusion of spathe and appendix. It is rather an effect of tight spiral enclosure by the valvule, co – operating with cohesion of the smooth surfaces by a mucous substance. This connection is very strong during early anthesis, but loosens later while the valvule starts wilting (Figs 29, 32). However, in *C. usteriana*, the loosening of the spathe appendix fusion is not found after all pollen has been released (Fig. 30). The appendix contains large vascular bundles.

3. Female Flowers

The stout gynoecia of *Lagenandra* are compactly arranged (Figs 5, 15, 16). They are linked together by the outgrowths on their surfaces (Figs 14, 15). These outgrowths are built from normal parenchyma and have a regular epidermis. Besides the mechanical fixation, they have no other function: they do not contain starch and neutral red reaction is negative.

4. Male Flowers

The male flowers consist of one or two sessile anthers (Figs 9 – 12). In *Lagenandra*, the thecae have a rim of special, astrablue staining, dense cells (Figs 10 – 12). The rim secretes clear droplets (Fig. 12). These droplets do not dry even though they are very small (circa 0.5 mm); thus they probably consist of fatty oils. In *Cryptocoryne* the anthers bear a rim of finger-like papillae (Fig. 8).

A conical or tubular stomium stands in the center of the thecae (Figs 8 – 12). The center of this stomium consists of the same kind of tissue as the rim of the anthers, staining strongly with astrablue, indicating hemicelluloses (Fig. 10). In young stages, the cells of stomium and anther rim are small and densely cytoplasmatic. At anthesis of the male flowers, the center of the stomia degenerates and collapses, so that the stomia become tubular (Fig. 13). The pollen and the matrix of the two connected pollen sacs exits through this tube. They form a little, yellow droplet at the end of the stomium (Fig. 2). The pollen is globular and smooth (Fig. 13). The matrix in the pollen sac is acellular and stains purple by fuchsine and astrablue. This implies that it contains proteins and hemicelluloses (Fig. 10).

5. Clubs

Club-like, sterile flowers are arranged above the fertile female ones (Figs 6, 16, 18 – 20), separated from male part of the spadix by the naked spadix stalk (Figs 5, 6). They are arranged spirally, densely packed and are yellow, bilobate, sometimes trilobate, by means of a median slit with paillae (Figs 18, 19). Intermediate forms between clubs and female flowers, as well as between clubs and male flowers, occur occasionally (Fig. 21). The tissue of the clubs is very dense (i. e. without any intercellular spaces). The clubs contain starch at early anthesis and are served by extensive vascular bundles (Fig. 19). The cells contain big nuclei and a dense, strongly fuchsine-stained cytoplasm, indicating high metabolic activity.

6. Anthesis

In the greenhouses at Zurich (45°N, 450 m above sea level), *Lagenandra ovata* flowers from July/August until December 1995. *L. praetermissa* begun flowering continuously in January 1996, and kept on until April 1996 after that it produced few flowers, probably depending on external circumstances.

The anthersis of *L. ovata* begins at about 18:00 until 21:00 with odor production and receptive stigmata. The inflorescence of *L. praetermissa* opens earlier in the afternoon (14:00) up to the evening. Heating of the spathe has not been recorded due to technical problems in *L. ovata*, but it can not be excluded. During the morning, odor production is reduced early (while the odor is perceptible for human noses until at least 24 hours after begin of anthesis). In *L. ovata*, the first male flowers shedding pollen (Fig. 12) are found in the afternoon after the beginning of anthesis (24 hours later).

7. Odor and Osmophores

At early anthesis of *Lagenandra ovata* and *L. praetermissa*, the external odor is like carrion of fish or like excrement, outside and inside the upper chamber of the spathe. This odor was confirmed independently by several persons. In the intact, anthetic inflorescence, the odor appears stronger inside the spathe chamber. In *L. ovata* and *L. praetermissa*, considerable amounts of liquid are found in the depression around the entry to the passage way to the kettle at anthesis (Figs 2, 3, 23). Isolated in a glass tube, it smells fishy, in both cases. In contrast to this, inside the kettle the odor is sweet, more like old fruits. It is weaker or is produced for a shorter time and is therefore not always as obvious as in the upper chamber.

The repulsive odor is produced by the spathe. The verrucate emergences are stained by neutral red, and therefore they may be osmophores: in *Lagenandra ovata* the emergences inside the spathe chamber are light and uptake of neutral red is obvious. Outside the chamber, they are darkly colored by anthocyanine and neutral red is not visible. In *L. praetermissa*, the emergences outside the spathe are light green (Fig. 23) and neutral red is distinct, while emergences are lacking inside.

The passage way of the ventile in *L. praetermissa* is positively stained by neutral red. In *L. ovata*, the dark color of the epidermis masks any vital staining of other parts of the spathe.

As observed by division of the spathe according to the methodical part, the spathe section surrounding the upper chamber smells strongly like dung or fish. The spathe part of the passage way and the spathe part surrounding the kettle smell the same, but weaker. This part of the spathe has a darker papillate apical part, and a light part basely functioning as a window - pane.

The fruity odor inside the kettle is produced by the spadix. The fertile male part of the spadix smells strongly like ripe peaches in *L. ovata*, and like mango or pineapple in *L. praetermissa*. In the anthers, the rim of *Lagenandra* (Figs 11, 10) and the papillae of *Cryptocoryne* (Fig. 8), respectively, stain deeply with neutral red (the rest of the anthers stain weaker in *Lagenandra* and *Cryptocoryne*). Because of this, secretory or osmophoric function of the anthers is expected.

The upper section of the female spadix, containing the sterile clubs, smells the same, but considerably weaker. This is perhaps due to an interrupted water supply for the clubs from the main axis, while male flowers still are attached to the spadix; or perhaps due to a bigger relative air volume, since it is the same vessel size as for the bigger male part of the spadix. The clubs of all *Cryptocoryninae* studied stain with neutral red (Fig. 20; simple vacuole staining is excluded, since vacuoles are smaller than in other tissues).

The stigmata are always stained with neutral red. This is not surprising, since stigmata are secretory, and dehiscing. In this case, osmophoric function of the stigmata is not proven by neutral red. The female section (without the sterile clubs) does not smell.

The valvule is in direct contact to the osmophoric zone at the base of the upper spathe chamber (Figs 5, 6, 28). In *Lagenandra*, it stains slightly with neutral red. In *Cryptocoryne usteriana* (Fig. 33), *C. purpurea*, *C.* cf. *consobrina* and *C. retrospiralis* (De Wit, 1982, personal observation), the valvule is yellow and strongly reacts to neutral red (Fig. 33). Thus, it has the function of an osmophore in *Cryptocoryne* (Vogel, 1963).

DISCUSSION

1. Diversification of Odor

The observation that *Cryptocoryninae* has a different odor outside and inside of the kettle is new. The odor outside of the kettle, i. e. in the upper chamber of the spathe and outside the inflorescence, is like carrion or dung. Inside of the kettle, a fruity odor dominates.

1). Olfactory Features of the Spathe

The carrion - like odor is produced by the spathe. Important are the rim - like and verrucate structures (Figs 3, 5, 22 - 24, 28). The verrucate emergences can be seen as accentuation of the horizontal, anastomosing rims on the adaxial surface of *L. ovata* and *L. praetermissa*. In *L. ovata* the rims show a continuous transformation into emergences at the base of the upper spathe chamber (Figs 3, 28). Similar emergences are found in other osmophores, such as on the flag of *Cryptocoryne griffithii*, *C. ciliata* (Vogel, 1963). Their extremely papillate nature is typical (Fig. 24). The reason for the clustering or for the elongation of the papilae probably is that they increase the active surface. The adaxial surface of the spathe is the major site of secretion, as is indicated by liquid accumulated there. But also the verrucate emergences on the abaxial, exposed side of the spathe (Figs 1 - 3) show osmophoric function (in *L. praetermissa*).

Engler (1920b) writers the acute papillae on the spathe epidermis are directed downwards in order to enhance the gliding down of trapped insects (Figs 25, 26). Knoll (1926) support this view by his studies on *Arum nigrum*. While in *A. nigrum*, the papillae are stout and densely packed, in *Cryptocoryninae*, they are long and acute (Fig. 25). In the passage way zone of *L. ovata* is the selecting bottleneck of the trap and it is said to be the place, where the pollinators are allowed to pass only in one direction (De Wit, 1970, 1982). Here the papillae are accompanied by reduced verrucate emergences (Fig. 26). In this region an insect claw may not find a hold on the trap wall due to the papillate surface, but it can still find a hold on the verrucate surface next to the papillate one in *Lagenandra*. The papillae of the spathe epidermis in *Lagenandra* do not prevent insects from escaping.

Since the entire passage way surface of *L. praetermissa* stains with neutral red, this papillate surface is assumed to function as an osmophore. This is also implied by Vogel (1963) who describes the papillate epidermis as a feature of osmophores. He mentions that dipters are lead by osmophore surfaces due to their chemotactic sensitivity, and that *Cryptocoryne ciliata* possesses such a papillate surface of the postgenitally fused spathe tube.

The valvule was described to move during anthesis and to close the kettle (De Wit, 1982). Such a movement is not observed in the *Cryptocoryninae* studied. A single inflorescence can not be opened and traced for a longer period without assuming artefacts of tender structures (such as wilting by drying). Slight differences in valvule position are perhaps a result of ageing. However, no movement of the valvule in the inflorescence was sufficient to close the valvule passage way significantly.

2). Diversification within the Spathe

The carrion - like odor is secreted by the spathe. It is not known whether the watery liquid exuded by the inner surface of the spathe is the odorous substance itself (Vogel, 1963 for *Cryptocoryne ciliata*). But the guttation starts and ends parallel to the odor perceptibility during the first 24 hours of the anthesis and according to the receptivity of the female flowers. In *Lagenandra*, the spathe varies in the amount of odor production. The inner surface is the dominant place, mostly the zone of the spathe emergences in *L. ovata* and the zone of the passage way in *L. praetermissa*. In correlation with the liquid, the spathe of *Lagenandra* forms a rim around the passage way (Figs 3, 23). The liquid is located in the depression around this rim, as if the rim was made to keep it from running into the passage way. In *L. ovata* not only one depression is formed, but many small ones by the bases of the emergences (Figs 3, 5).

3). Flowers as Osmophores

The female flowers never produced any perceptible odor in *Lagenandra*. A failure due to a lack of water supply can be excluded, because the detached male part still does produce odor, even though it has no bigger water storing capacity than the massive, female part. In *Lagenandra ovata*, the fruity smell of the kettle is produced mainly by the fertile male flowers. They are identified as osmophores by neutral red staining of their peripheral rims and the stomia, as well as by odor examination according to the methodical part. The peripheral rim of the thecae secretes small droplets at anthesis. Unlike the much bigger drops at the end of the stomia, these droplets are clear (Fig. 12). In *Cryptocoryne*, this rim is papillate (Fig. 8). Microscopically the cells in the rim and the cells in the stomium tube are similar: both are stained densely blue with astrablue (Fig. 10). They stain neutral red, probably due to their dehiscence. This does not imply they are not osmophores, because dehiscence and secretory function are linked in osmophores (Vogel, 1963). Further, the male flowers (and even more the sterile clubs) contain large amounts of starch, dense cytoplasm, no concentrated vacuole and expanded nuclei (Figs 10. 19), which are features of osmophores mentioned by Vogel (1963).

The sterile clubs on top of the female part of the spadix show features of osmophores as well (Vogel, 1963). De Wit (1970, 1982) and Sivadasan (1985) describe the clubs *in Cryptocoryne* as osmophores (Fig. 17). The sterile clubs probably contribute to the odor in a higher amount than expected from the snap cap observation: the clubs were detached from the rest of the spadix, and water and energy supply were interrupted. The fertile organs of the spadix were still in contact to the spadix mass and to its stored water. Vogel (1963) stresses the importance of water and energy for osmophores. This is confirmed by the two relatively large branches of vascular bundles reaching into the lobes of the sterile clubs in *Lagenandra* (Fig. 19). But as opposed to De Wit (1982), the clubs produce not the carrion - like odor but the sweet one, as the fertile male flowers do. Similar yellow sterile clubs above the female part of the spadix are found in other members of the

Areae as well, e. g., *Typhonium*, *Biarum*, *Plesmonium* and in *Sauronmatum guttatum* (Engler, 1920b; Meeuse *et al*, 1984).

In *Sauromatum guttatum* their function has been studied in detail by Chen et Meeuse (1971). As in *Cryptocoryninae*, the sterile clubs are located closely above the female flowers. Unlike in *Sauromatum*, the tissue of the clubs is highly dense in *Cryptocoryninae* (Fig. 19).

According to Vogel (1963), the intercellular spaces are responsible for the oxygen supply by diffusion. The clubs in *Cryptocoryninae* are so small in respect to those in *Sauromatum*, that diffusion may be sufficient without intercellular spaces. In *Arum maculatum* the different smell (of germacrene) inside the kettle is probably produced by the fertile portion of the spadix (Kite, 1995).

4). Comparison with *Cryptocoryne*

De Wit (1970) writes, that the carrion – like smell of *Cryptocoryne* turns to sweet sometimes. However, in *Sauromatum guttatum*, the sweet components remain perceptible in the kettle after the appendix is no longer active (personal observation).

In *Lagenandra ovata*, *Cryptocoryne alba* and *C. ciliata* (Vogel, 1963; De Wit, 1982), the constricted zone of the spathe has a large fold and verrucate emergences (Figs 3, 5). Even the watery exudate on the odor producing parts of the spathe is described for *Cryptocoryne ciliata* by Vogel (1963).

The flag of *C. ciliata* bears elongate emergences and *C. griffithii* verrucate emergences (Vogel, 1963). They are clearly products of the adaxial spathe surface (Vogel, 1963) and have the same position and look like the verrucate, papillate emergences in *Lagenandra ovata* (Figs 5, 22, 24, 26). The emergences occur along the margin and obviously they are the origin of secretion of the odorous, watery liquid in *L. ovata* and in *C. ciliata* (Vogel, 1963). Vogel (1963) noticed that it is not only this marginal region that produces odor, but the entire adaixal lamine.

The valvule of several *Cryptocoryne* is yellow (Fig. 33; De Wit, 1982) like the male flowers and sterile clubs, and stains positively with neutral red. Thus, this valvule produces odor, too (Vogel, 1963). While the osmophore of the spathe is still continuous in *Lagenandra* and *Cryptocoryne* spiralis, in other species of *Cryptocoryne*, osmophoric function is divided distinctively into the apical, free margins of the spathe tube (flag. Fig. 31) and the valvule. The odor of the two osmophores may differ. Both osmophores, verrucated ones and valvule, are formed by the spathe margin.

REASONS FOR ODOR DIVERSIFICATION

As Vogel (1963) and Faegri et Van der Pijl (1979) point out, sapromyophilous blossoms do not attract their pollinators by rewarding them and giving a clue to learn the key to the reward, as e. g. typical for hymenopters. Rather they manipulate the instinct directly. Therefore, the attracting substances are strictly specific for the behavior of visiting species.

Pitcher trap blossoms depend on dipters or beetles. It is remarkable, that the odor correlates with the medium of oviposition of the pollinator (Knoll, 1926; Vogel, 1963; Meeuse, 1978; Faegri et van der Pijl, 1979; Meeuse *et al*, 1984; Banziger, 1991; Bay, 1996). Banziger (1991) interprets the unpleasant smell in *Rafflesia kerrii* as specifically inducing search behavior for oviposition sites by carrion flies (also Beaman et al, 1988). Chemoreceptors were found on the ovipositor of several sarcophagous dipters (Rice, 1977). The flies of these studies are quite big and act as efficient long distance pollinators (Banziger, 1991). In *Sauromatum guttatum*, the stench obviously attracts carrion and manure – dependent insects (Meeuse et al, 1994).

Some of the steroids compounds imitate hormones. This is perceived even by human noses; e. g. *Arum maculatum* smelling like human urine (Vogel, 1963). Single compounds can be identified as semiochemicals. Kite (1995) found 2 – heptanone and p – cresol in the appendix – secreted odor of *Arum maculatum*. These substances are hormones and pheromones for mating, alarm, attraction or ovipostition in various insects, including coleopters and dipters. This advertisement of a site for oviposition is correlated mainly with the long distance attraction (Banziger ,1991; Bay, 1996). Indoles and amine – containing components are perceptible in very low concentrations (R. Kaiser, personal communication). Since insects are very sensitive for specific substances, carrion – or dung – dependent insects may have an even higher sensitivity for specific components. Such components are perfect to attract a narrow spectrum of visitors over long distances. Narrow, in this context, means the range of breeding and perception behavior, not the phylogenetic relationship.

When the pollinator enters the blossom, the key attractor changes to fruity components in *Sauromatum*, *Lagenandra* and *Arum*, typical for carbohydrate rich food sources. Banziger (1991) interprets in *Rafflesia kerrii* the sweet one to "advertise carbohydrates". In *Sauromatum guttatum*, the sweet odor inside the kettle "may be the stimulation of mating of visiting beetles" (Meeuse *et al*, 1994).

Over short distances, the fruity character of terpenoid components guides the way down into the trap. This is in co – operation with fecal compounds, which inactivate the claustrophobia of dipters (Banziger, 1991). Considering that dipters and beetles have a narrowly programmed behavior in blossoms (Vogel, 1963; Beaman *et al*, 1988; Pellmyr et Patt, 1986; Patt *et al*, 1992), this implies a change of the programming of the visitor from oviposition to searching for food (Chen et Meeuse, 1971; Meeuse, 1978; Banziger, 1991; Kite, 1995). The success of this method is proven by the enormous number of visitors gathering in the kettle: first they are attracted and second they are guided to the right place where they stay. In *Sauromatum guttatum*, the visiting flies can see the way out (since you can see them through the spathe constriction, personal observation). Shaking of the inflorescence may cause a few single flies to leave the kettle and climb up the appendix or the spathe. But they return immediately into the trap (personal observation).

2. Pollen Matrix

The pollen is smooth and globular, since an exine sculpture would hinder the passage through the stomium tube (Fig. 13). In *Cryptocoryne*, and *Lagenand*ra, pollen is released at the end of the tubular stomia in a mucous matrix forming a droplet similar to Rafflesia (De Wit, 1982; Beaman *et al*, 1988; Banziger, 1991) (Fig. 12).

The pollen probably is attached to the pollinators by the mucous liquid, as in *Rafflesia* (Beaman *et al*, 1988; Banziger, 1991). It is not known, whether the pollinators eat the mucous liquid. For *Rafflesia kerrii*, which also releases pollen in a mucous matrix, such a reward by a mucous matrix to carrion flies is reported, in combination with a mucous secretion at the base of the trap chamber (Banziger, 1991).

According to Beaman *et al*. (1988) for *Rafflesia* pollination, blossoms rewarding their visitors might have evolved from deceptive blossoms, but do not parasites the pollinators as proper 'carrion blossoms' do according to Faegri et van der Pijl (1979). Lasting parasitism is possible only, if the parasite (i. e. the blossom) is not too frequent, since its pollination consumes time of the pollinators lifespan, reducing their fitness and availability. If a blossom is more frequent, changes to lower costs for pollinators may occur, i.e. a symbiosis is developed. *Rafflesia kerrii*, even though rare, already shows rewards for pollinators (Banziger, 1991). Such efficient pollinators are also associated with other aroids (Bay, 1996). Nectar reward was found in *Aristolochia grandiflora* by Cammerloher (1923). It is suggested in *Arum dioscoridis* and *A. maculatum* (Knoll, 1926), which are pollinated by smaller insects with shorter pollen transfer distance. Also *Amorphophallus variabilis* was found to offer a starchy food tissue to *Nitidulidae* (Van der Pijl, 1937). *Nitidulidae* are small pollinators. Thus for *Cryptocoryninae* with small pollinators, pollinator reward is not exceptional. Perhaps frequency of anthetic inflorescence in a habitat compensates for the pollnators weakness in respect to long distance transfer.

3. Outlook

Differential odor production is expected in diverse sapromyophilous species of the Araceae, e. g. other *Aroideae*, *Colocasioideae*, *Philodendroideae*, and in pitcher trap blossoms in general. The discovery of further examples of odor diversification and the reaction of insects to chemical substances might provide a better understanding of sapromyphilous trap blossoms.

There are sterile structures in various aroid inflorescence. In *Arum*, most species show two groups of sterile organs (beside the appendix): one above and one beneath male flowers. Olfactory diversification was shown by Kite (1995) for *A. maculatum*. In some species of *Arum*, the sterile organs are not functional barriers in the manner described by Knoll (1926). They share features with osmophores and probably contribute to the odor in the kettle.

Pistia shows a collar – like structure around the free part of the spadix beneath the male flowers and further down, a horse shoe – shaped scale. Both secrete droplets (Buzgo, 1994). Obviously, sterile floral organs in Araceae are tendentially osmophores.

The remaining questions are: In which taxa does differential odor production occur in Araceae, and in sapromyophilous blossoms, in general? Is there a correlation of this pollination syndrome and the odor differentiation? What are the most common odorous substances? Is the function as osmpohores in aroids correlated with the ontogenetic program of male flowers (Chen et Meeuse, 1971)? Are functional osmophores in Araceae expressions of genes, originally regulating the male anthetic catabolism.

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Explanations of Plates

Buzgo M., Odor Differentiatation in *Lagenandra ovata* (Araceae) Plate Ⅰ

1. Inflorescence of *Lagenandra ovata*, a few hours before opening of the spathe; × 0.4. 2. Inflorescence of *Lagenandra ovata*, opened longitudinally, K = kettle, U = upper spathe chamber; × 0.4. 3. Terminology used on inflorescence organs of *Lagenandra ovata*, modified after De Wit (1982): K = kettle, L = tip of the spathe, R = roof, Y = margins of the spathe and emergences, Z = emergences; × 0.4. 4. Inflorescence of *Cryptocoryne spiralis*; × 0.9. 5. Kettle of *Lagenandra ovata*: F = female part of the spadix, M = male part of the spadix, P = passage way, R = roof, V = valvule, Z = emergences; × 1.2. 6. Terminology used on inflorescence organs in the kettle of *Lagenandra ovata*, modified after De Wit 1982: A = appendix, C = clubs, F = female part of the spadix, M = male part of the spadix, N = naked part of the spadix, P = passage way, R = roof, V = valvule; × 1.2.

Buzgo M., Odor Differentiatation in *Lagenandra ovata* (Araceae) Plate Ⅱ

7. Appendix of *Lagenandra ovata*; × 11.6. 8. Theca of *Cryptocoryne usteriana* with papillate rim and horn – shaped stomium (not yet open); × 116. 9. Male flowers of Lagenandra praetermissa: basely, flowers are dimmer but the anthers are monothecate (⬆); × 11. 10 Male flower of *Lagenandra ovata*, longitudinal section: S = stomia, R = rim; × 11. 10. Male flower of *Lagenandra ovata*, longitudinal section: S = stomia, R = rim; × 45. 11. Theca of *Lagenandra praetermissa* with rim and horn – shaped stomium (not yet open); × 59. 12. Anther of *Lagenandra praetermissa* with droplet atop of the stomia: P = pollen, R = rim; × 104.

Buzgo M., Odor Differentiatation in *Lagenandra ovata* (Araceae) Plate Ⅲ

13. Male flower of *Cryptocoryne usteriana* in longitudinal section: S = stomia with pollen grains in its tube, R = papillate rim; × 86. 14. Single female flower of *Lagenandra ovata* with lateral emergences and a broad, papillate stigma; × 40. 15. Female flowers of *Lagenandra ovata* in longitudinal section, linked together by emergences (⬆); × 26. 16. Female part of the spadix of *Lagenandra ovata*: C = clubs; × 3.9. 17. Sterile clubs of *Cryptocoryne usteriana*, atop of the female flowers; × 41.

Buzgo M., Odor Differentiatation in *Lagenandra ovata* (Araceae) PlateⅣ

18. Club of *Lagenandra ovata*, two-lobed with papillae in the center; × 59. 19. Club of *Lagenandra ovata* in transversal section: periphery with dense cytoplasmatic cells (D), centrally with a division and strong bundles (⬆); × 34. 20. Female part of the spadix of *Lagenandra ovata* after neutral red staining: F = gynoecia, ⬆ = clubs; × 3.9. 21. Club of *Lagenandra ovata*, one half is yellow with club features (C), the other half shaped as a gynoecium (F); × 69. 22. Spathe of *Lagenandra ovata*, inner surface and margins (still fused) with emergences (Y) and riffles (X); × 1.5. 23. Inflorescence of *Lagenandra praetermissa*: K = congenitally fused spathe forming the kettle, ⬆ = depression around the passage way; × 0.5.

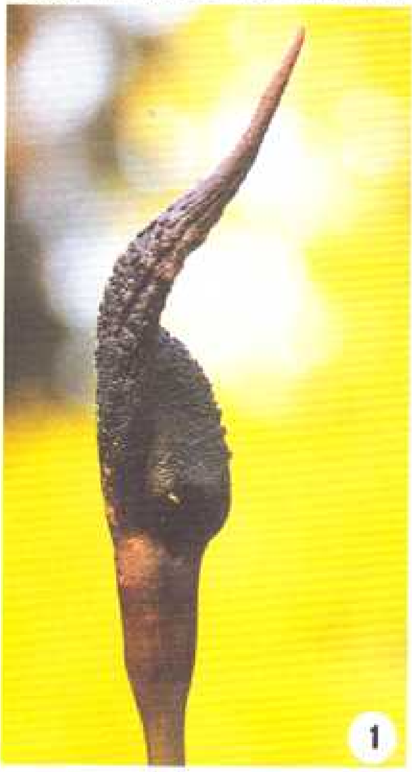
Buzgo M., Odor Differentiatation in *Lagenandra ovata* (Araceae) Plate Ⅴ

24. Emergence on the spathe constriction of *Lagenandra ovata*; × 77. 25. Acute papillae on the inner surface of the spathe in *Lagenandra ovata*; × 276. 26. Acute papillae on the inner surface of the spathe margins in *Lagenandra ovata*: A = papillae, Y = emergences; × 16. 27. Young spadix of *Lagenandra ovata*: V = valvule, M = male flowers, F = female flowers; × 16.28. Valvule and passage way of *Lagenandra ovata*: A = acute trichomes, J = inner spathe margin, P = passage way, V = free valvule lobe, Y = emergences; × 13.

Buzgo M., Odor Differentiatation in *Lagenandra ovata* (Araceae) Plate Ⅵ

29. Male part of the spadix and appendix surrounded by the spathe valvule in *Lagenandra ovata*, stained neutral red; × 3.9. 30. Male part, appendix and valvule of *Cryptocoryne usteriana* in longitudinal section: A = appendix, M = male flower, V = valvule; × 43. 31. Inflorescence of *Cryptocoryne usteriana*, U = spathe fused to a tube, T = yellow flag-like exposed part of the spathe; × 1. 32. Aspect onto the center of the valvule spiral in *Cryptocoryne* cf. *consobrina* from above: f = zone of postgenital fusion of valvule lobe to the proper spathe, P = passage way, Z = central hole where the appendix contacts the upper chamber of the spathe; × 94. 33. Male part of the spadix of *Cryptocoryne usteriana*, with appendix (⬆) and yellow valvule; × 15.

Buzgo M., Odor Differentiatation in *Lagenandra ovata* (Araceae) Plate I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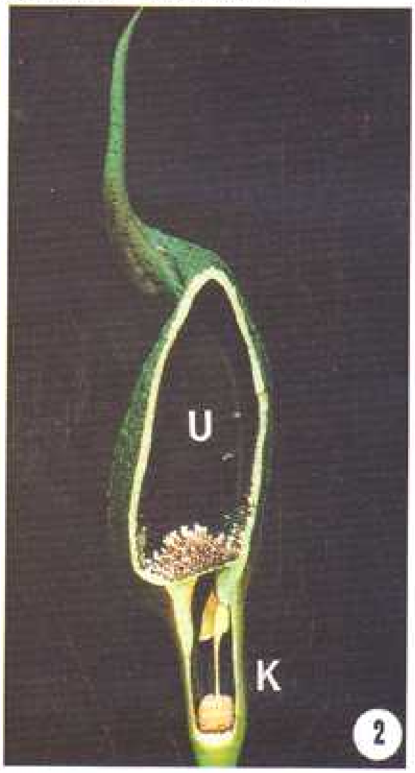

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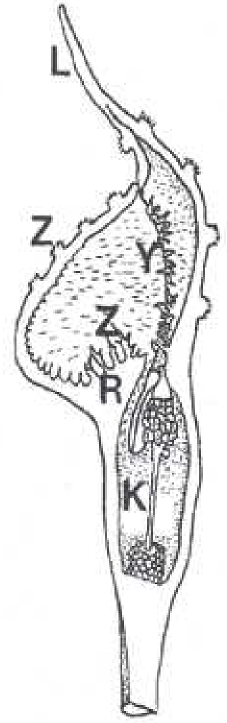

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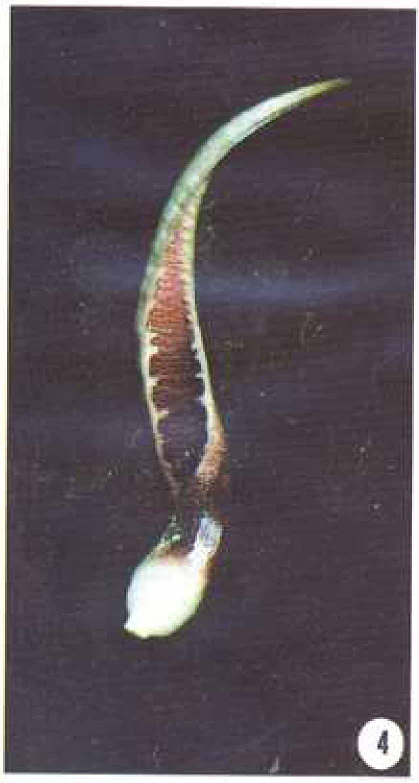
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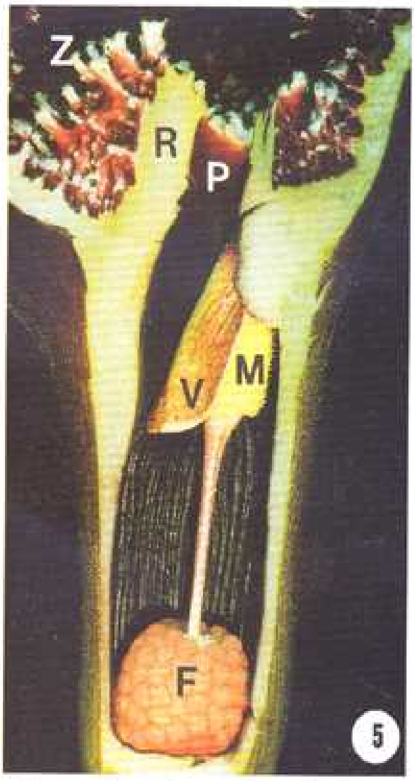

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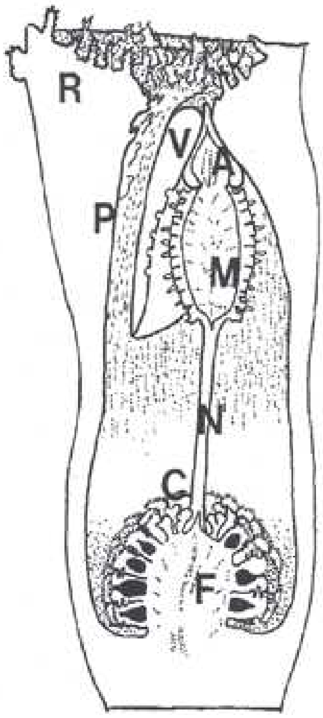

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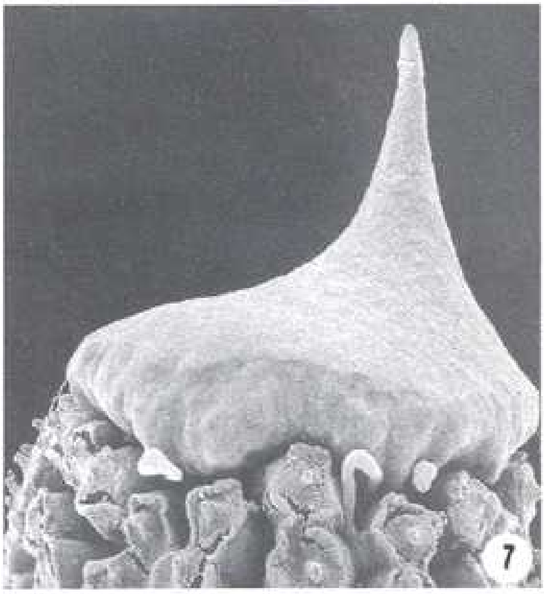
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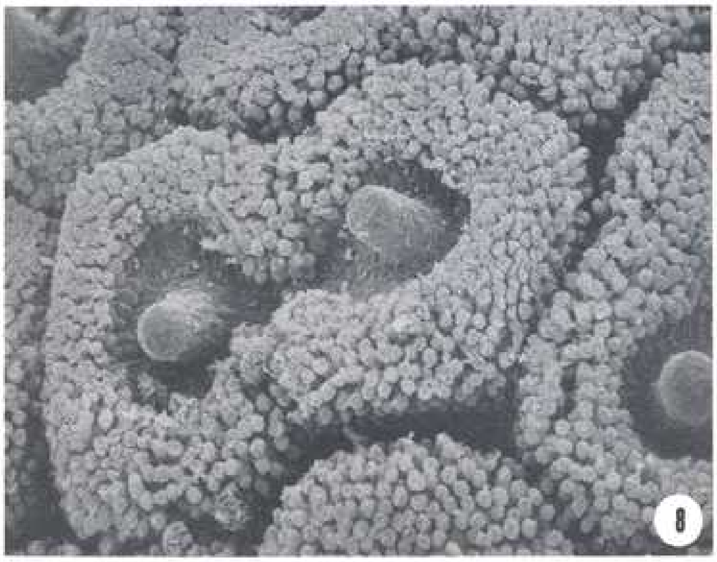
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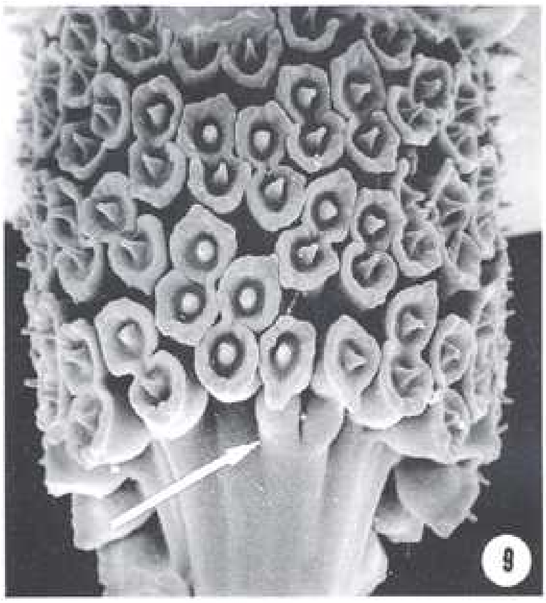
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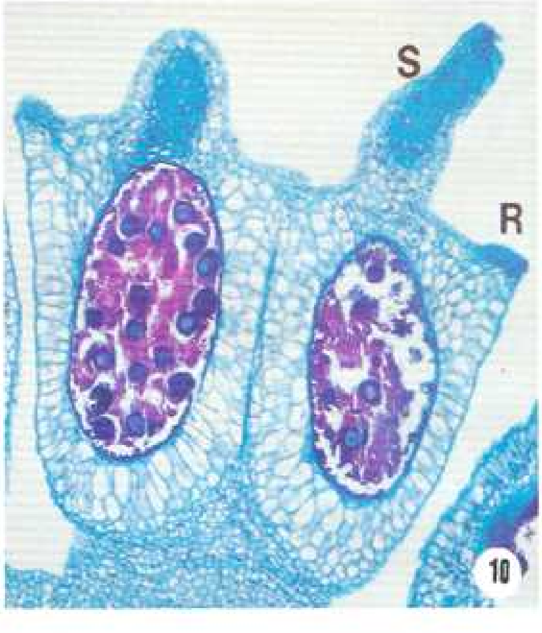

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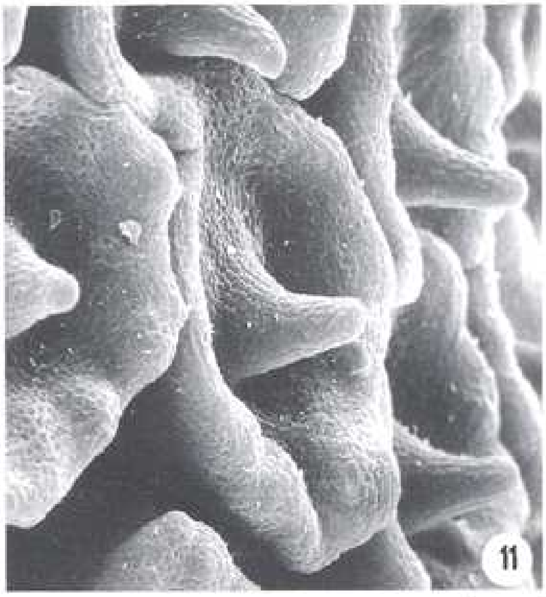
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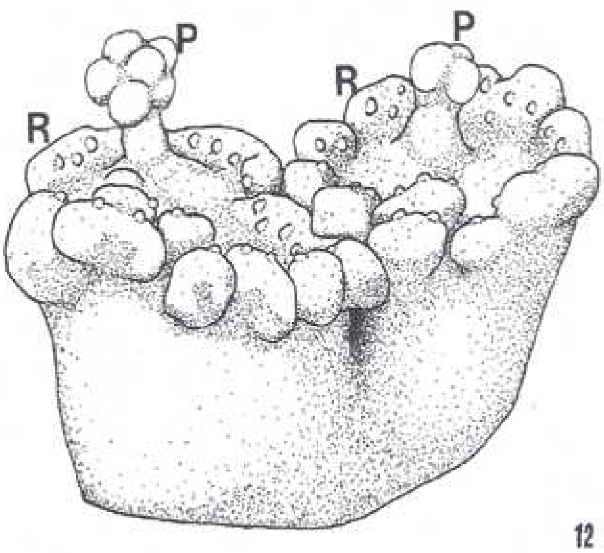

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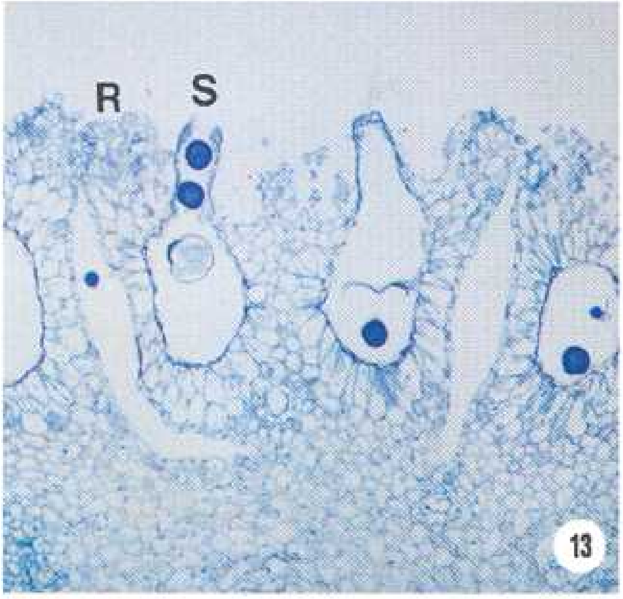

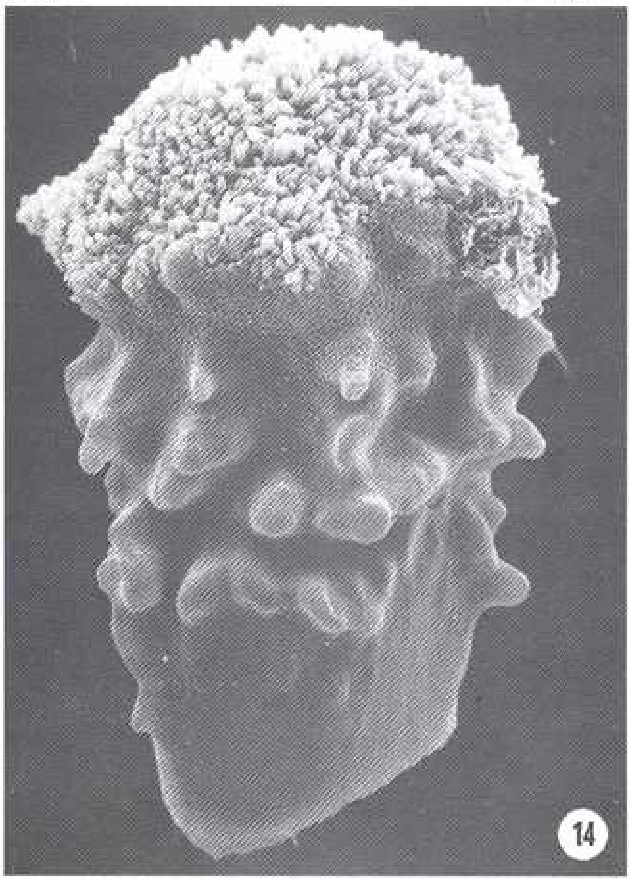

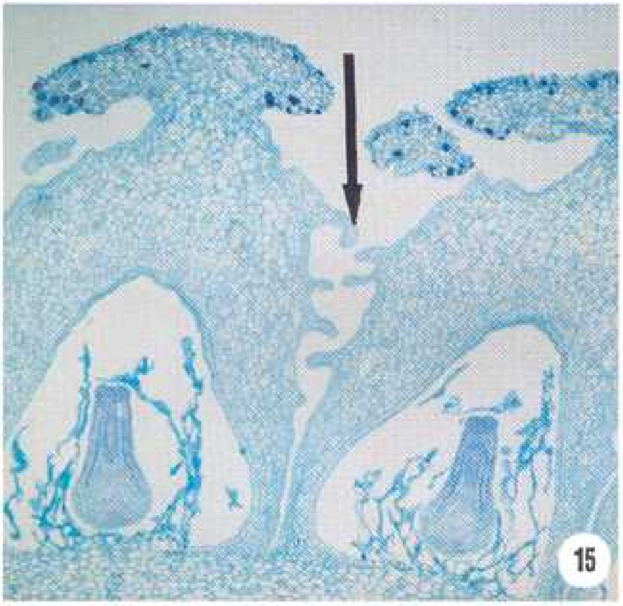

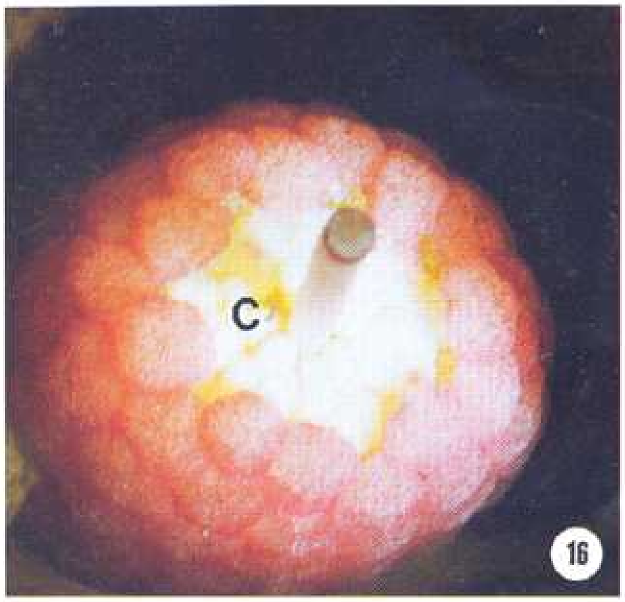

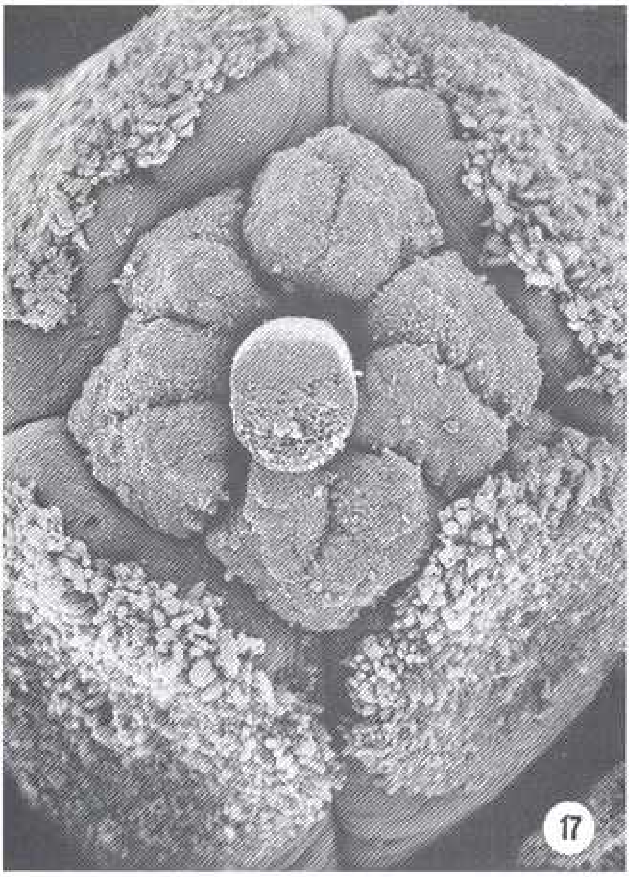

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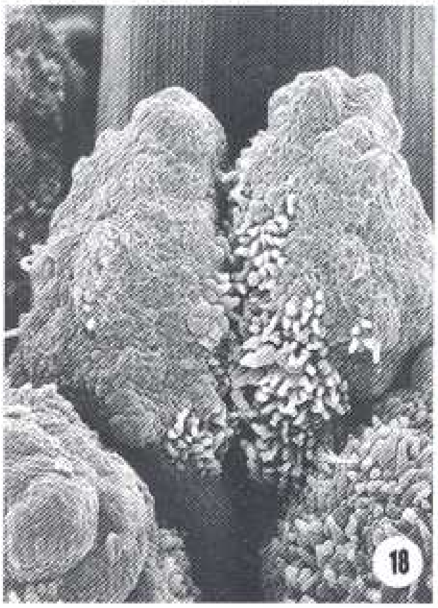

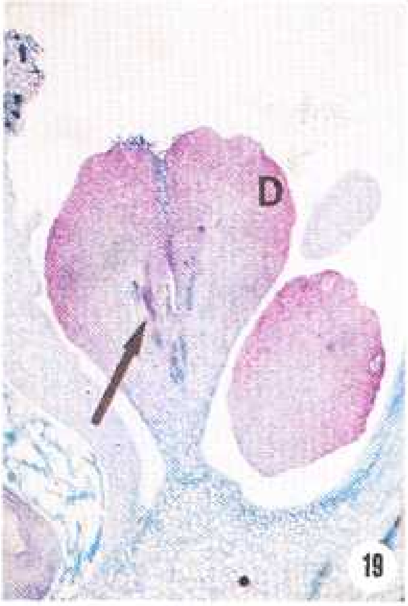

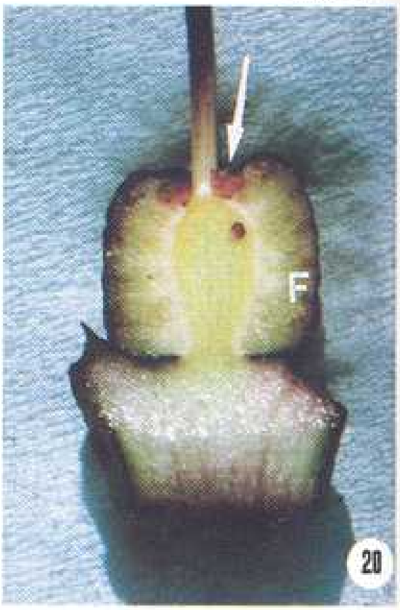

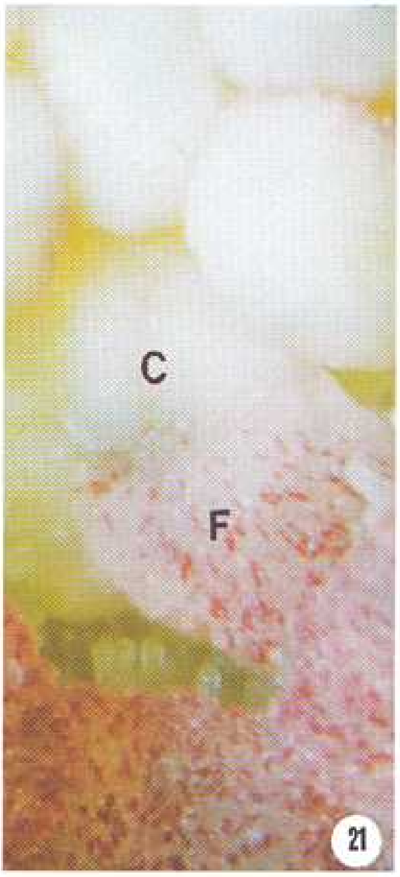

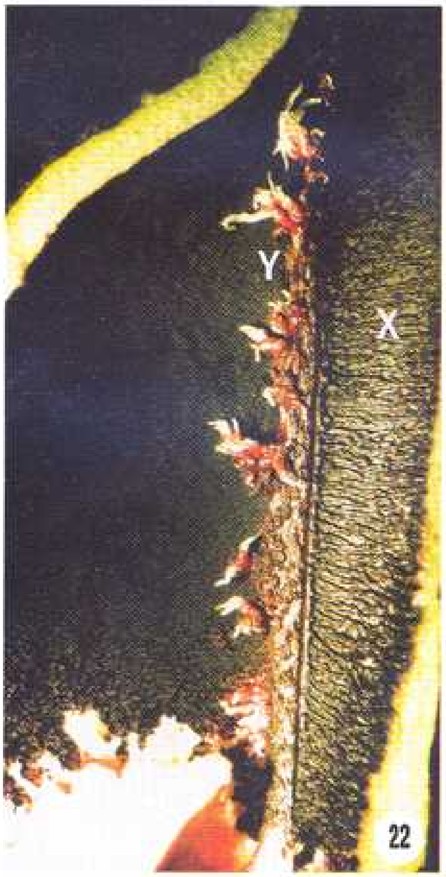

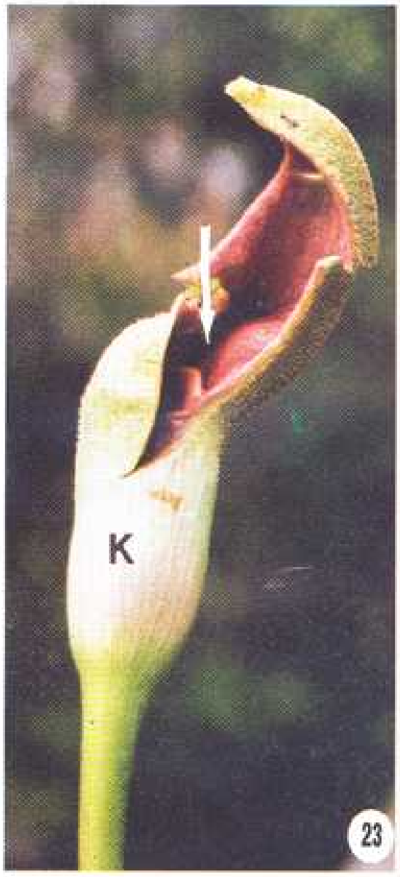

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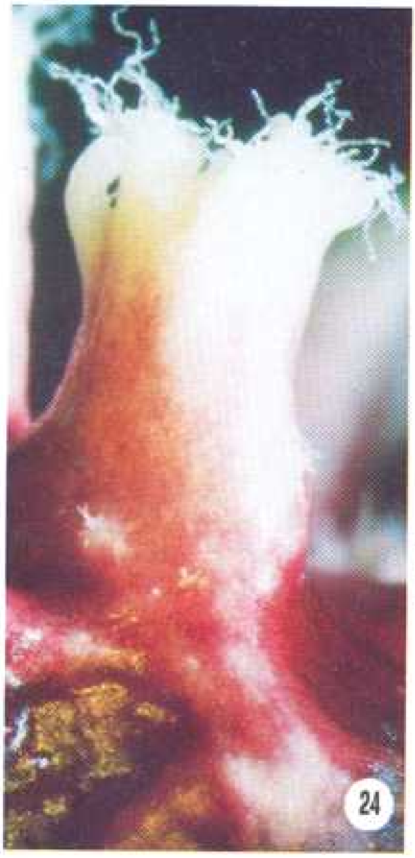
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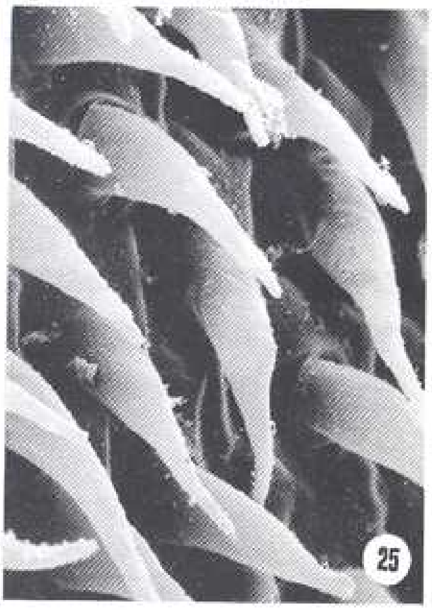
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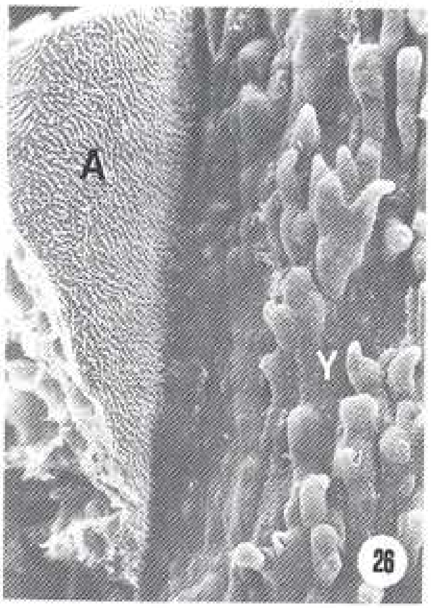

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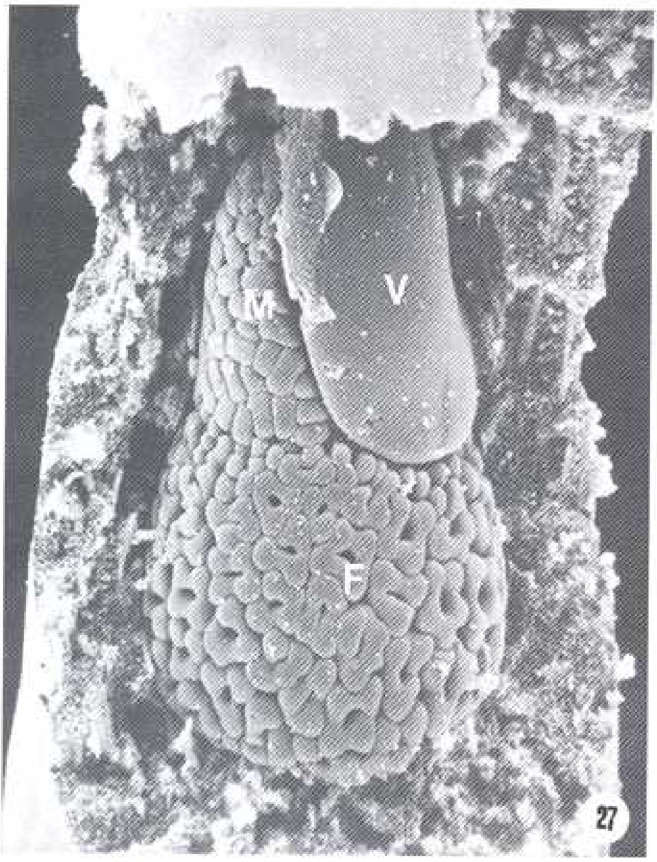

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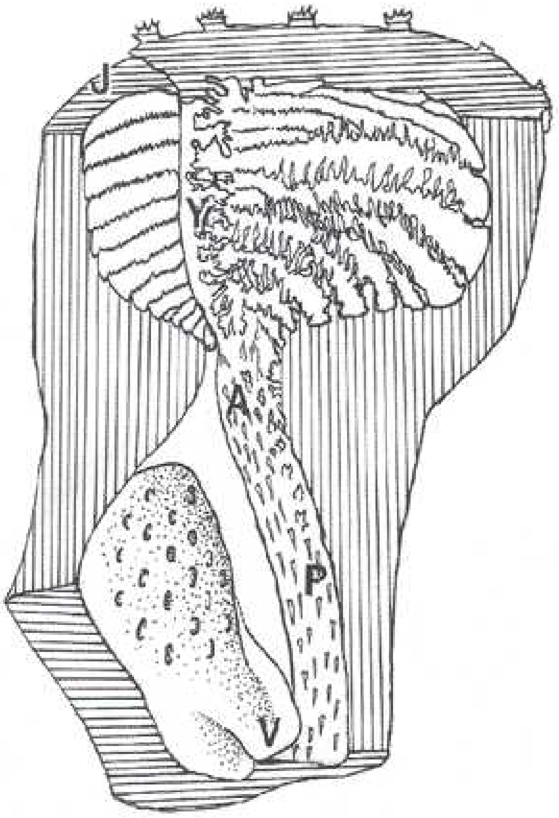

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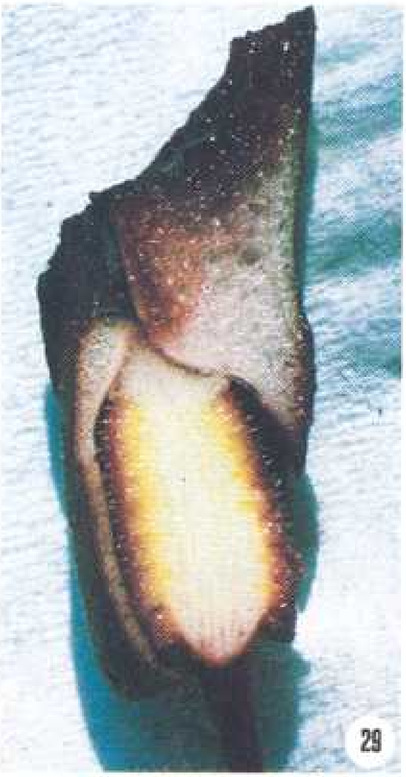
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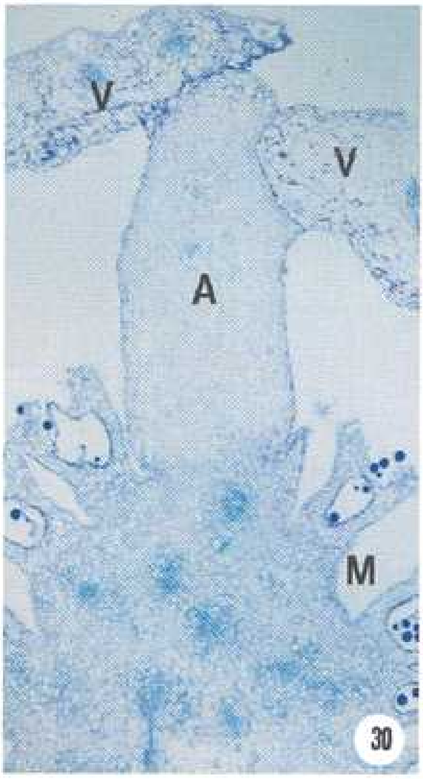

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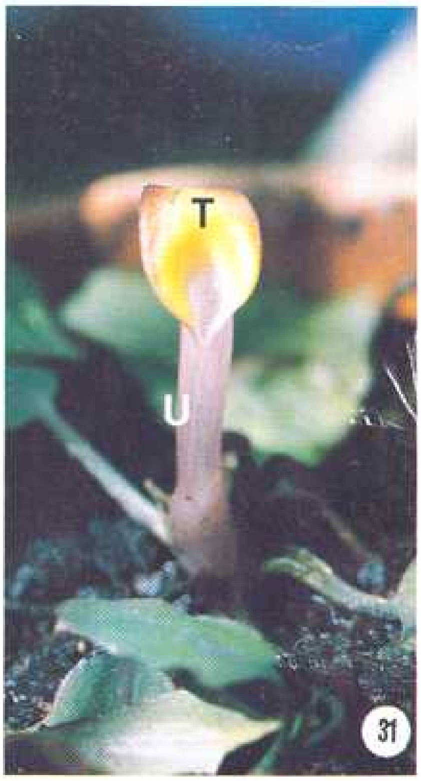

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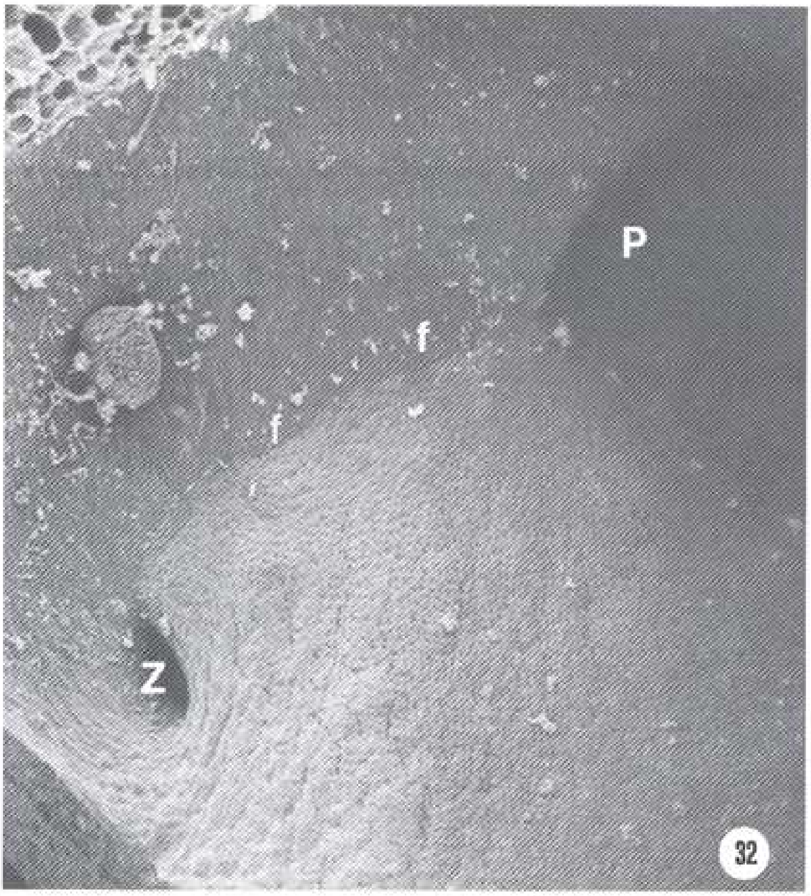

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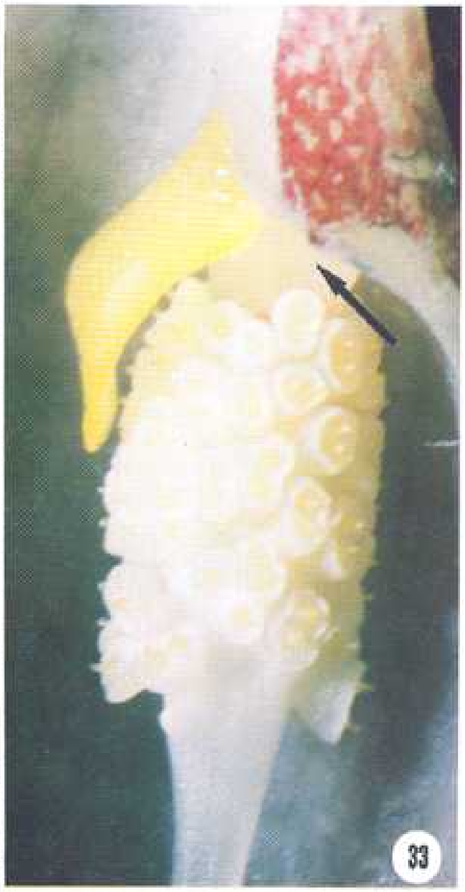
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